

AN INVESTIGATION INTO THE STATUS OF *IRIS THOMPSONII* (IRIDACEAE)

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ABSTRACT

Within *Iris* series *Californicae*, experimental hybrids between species are readily produced and natural hybrids have been reported as common. *Iris thompsonii* from the northwestern slopes of the Klamath Mountains has been described as a natural hybrid between *I. douglasiana* and *I. innominata*. The purpose of this study was to investigate the relationships of these three species and in particular to determine the status of *I. thompsonii*. Methods used were discriminant and cluster analyses of morphological characters and a chemotaxonomic analysis of flavonoid pigments using thin layer chromatography. The thirteen populations studied were found to represent three species: *I. douglasiana*, *I. innominata*, and *I. thompsonii*. This study does not support the current taxonomy for *I. thompsonii* that places this taxon within *I. innominata* as a color form or occasional hybrid between *I. innominata* and *I. douglasiana*.

The series *Californicae* (Diels) G. Lawr. in the genus *Iris* (Iridaceae) comprises approximately 16 closely related taxa that are thought to form a natural group. These taxa are distributed along the Pacific Coast in Washington, Oregon, and California. Numerous studies (e.g., Foster 1937; Lenz 1958; Clarkson 1959; Carter and Brehm 1969) have cited the occurrence of intraspecific variation and interspecific hybridization as sources of confusion in the systematics of the series.

The taxa under consideration in this study, *Iris douglasiana* Herbert, *I. innominata* L. Henderson, and *I. thompsonii* R. Foster, are found in the Klamath Mountains of southwestern Oregon and northern California. A major serpentine soil area occupies much of the study site. Serpentine areas are characterized by infertile, sparsely vegetated areas and species rich, endemic floras. Speciation in serpentine floras is thought to result from edaphic factors, specifically a combination of heavy metal toxicity and low nutrient levels (Kruckeberg 1954, 1986; Walker 1954). The three species occupy different habitats within this region. *Iris douglasiana* is typically found on grassy headlands along the coast, rarely more than two kilometers inland. *Iris innominata* inhabits inland rocky mountainous sites with sparse vegetation. *Iris thompsonii* is also an inland species but occurs on less sparse sites where a grass understory is generally present.

The series *Californicae* is often separated into three groups based

on perianth tube length. The intermediate perianth tube group consists of only these three species. *Iris douglasiana* is easily recognized by its large stature, wide leaves, and inflorescences with several flowers. Differences between *I. innominata* and *I. thompsonii* are less obvious and have led to some controversy. Both species are rather small with relatively narrow leaves and one (or sometimes two in *I. thompsonii*) flowers. Flower color in all three species has been reported to be variable. The most recent studies of the taxonomic relationships of the species did not lead to a consensus. Lenz (1958, 1959a) recognized *I. douglasiana* and *I. innominata* but retained *I. thompsonii* within *I. innominata*, considering some populations to be a hybrid between the two species and others to represent a color form of *I. innominata*. Clarkson (1962) retained *I. thompsonii* as a separate species although he considered it a probable hybrid between *I. douglasiana* and *I. innominata*. The purpose of this study was to investigate the status of these three species—within their area of sympatry.

Numerical analyses of selected characters and flavonoid studies were undertaken to: 1) determine what taxa are represented by the populations studied; 2) evaluate the relative amount of intra- and interspecific variation present; and 3) investigate the possible hybrid origin of *I. thompsonii*.

METHODS

Thirteen populations (Table 1, Fig. 1) representing the range in which the three species can be found sympatrically were chosen as study sites. All of the study populations are located in southwestern Oregon except the Smith River population from adjacent Del Norte County, California. *Iris thompsonii* is known from just south of Powers in Coos County, Oregon, southward into northern Del Norte County, California. The range of *I. innominata* is entirely within Oregon in the northern portion of the study area from just west of Iron Mountain in Curry County, Oregon, eastward to Wolf Creek in Douglas County. *Iris douglasiana* is found along the coast from Coos Bay in Coos County south to Santa Barbara County, California. The three species are sympatric in the northern part of the study area to the west and to the south of Iron Mountain. *Iris thompsonii* and *I. douglasiana* are also sympatric in the southern portion of the study area along the Rogue and Smith rivers.

Numerical Studies. Floral and vegetative parts were collected from 10 to 25 individuals per population during the years of 1981, 1982, 1984, 1985, 1987, and 1988. Measurements taken were: stem length, number of cauline leaves, leaf width, number of flowers per inflorescence, bract length, bract width, petal length, petal width, sepal length, sepal width, stigma length, stigma width, stigma lobe length,

TABLE 1. COLLECTION SITE DATA FOR THIRTEEN POPULATIONS OF *IRIS* SPECIES FROM SOUTHWESTERN OREGON AND NORTHERN CALIFORNIA (Fig. 1). ¹Forest Service Rd 333 is the road between Agness and Powers. ²Forest Service Rd 325 is the road between 333 and Humbug Mountain State Park.

Population	Collection data
Daphne Grove	OR: Coos Co., 2.4 mi S of Daphne Grove Campground on Rd 333 ¹ .
Iron Mountain I	OR: Curry Co., 0.5 mi S of county line on Rd 333.
Road 333	OR: Curry Co., 5.1 mi S of county line on Rd 333.
Road 3400	OR: Curry Co., 450 yd. E along rd on N bank of Shasta Coast Cr.
Road 3406	OR: Curry Co., 0.8 mi E along rd on N bank of South Cr.
Cape Blanco	OR: Curry Co., Cape Blanco Park.
Iron Mountain II	OR: Curry Co., 11 mi W of junction with Rd 333 on Rd 325 ² .
Champion Park	OR: Curry Co., roadbank at Champion Park.
Meyers Creek	OR: Curry Co., where Meyers Cr. crosses U.S. 101.
Carpenterville	OR: Curry Co., 8.1 mi N of U.S. 101 on Carpenterville loop.
Snaketooth	OR: Curry Co., 19.5 mi E of U.S. 101 along rd following the main fork of the Chetco R.
Chetco River	OR: Curry Co., 4 mi E of U.S. 101 along rd on N bank of Chetco R.
Smith River	CA: Del Norte Co., Jedediah Smith State Park.

peduncle length, and perianth tube length. A qualitative evaluation of flower color also was recorded.

Cluster analysis was employed using a modification of Hartigan's K-Means program. Individual plants were used as operational taxonomic units (OTU's) and a total data set of 207 OTU's were analyzed. The program executed ten internal iterations and computed a maximum of ten clusters using zero as a starting point. Flower color was entered as ordinal data from 0 to 5 for yellow (white to yellow) and purple (white to purple). A discriminant analysis of the data set was generated by use of the SYSTAT DISCRIM program. Finally a tree diagram illustrating the relationships of the populations studied was generated using euclidean distances and single linkage methods (SYSTAT JOIN). Mean population values were entered for each character.

Flavonoid Studies. Petals, sepals, and stigmas from 10–20 individuals were collected from ten of the study populations and flavonoids were extracted in acidified methanol for 36–48 hours under refrigeration (Parks 1965). Approximately 20 μ m of extract was applied to Analtech Avicel F cellulose thin layer plates for simultaneous development. TBA was used for both directions (6:2:1 and 3:1:1 respectively). The dried plates were observed under long- and shortwave UV light and marked for pigment spots. Spectral data of pigment spots were obtained by removing the spot from the plate

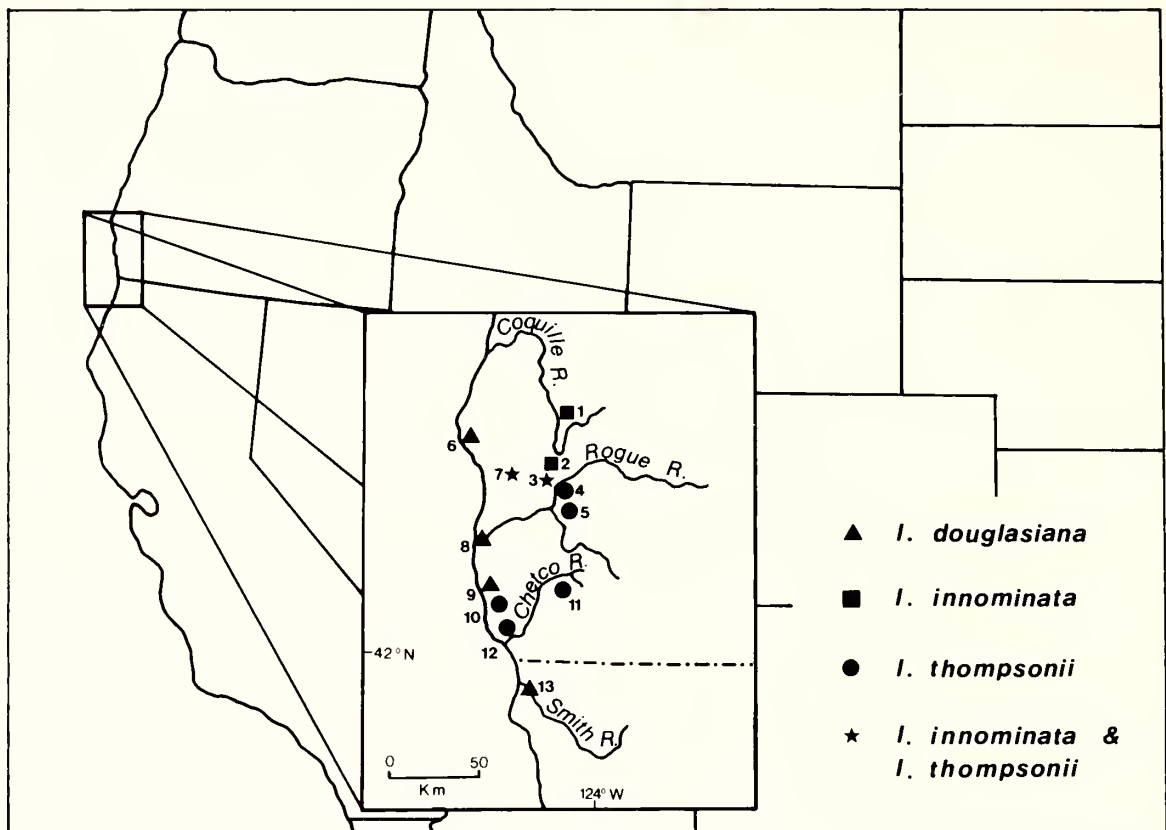


FIG. 1. Study populations of three *Iris* species from southwestern Oregon and northern California. 1. Daphne Grove. 2. Iron Mountain I. 3. Road 333. 4. Road 3400. 5. Road 3406. 6. Cape Blanco. 7. Iron Mountain II. 8. Champion Park. 9. Meyers Creek. 10. Carpenterville. 11. Snaketooth Road. 12. Chetco River. 13. Smith River.

and extracting the pigment in acidified methanol. A Beckman DU-7 spectrophotometer was used for gathering spectral data.

RESULTS

Numerical Studies. Three clusters were found to be optimum, as the mean distance to cluster centers decreased by 42.3% with the formation of a third cluster but the mean distance only decreased by 2.0% when a fourth cluster was formed. *Iris douglasiana* was represented by Cape Blanco, Meyers Creek, Smith River, and Champion Park populations. Daphne Grove and Iron Mountain I populations formed a cluster representing *Iris innominata*. Carpenterville, Chetco River, Snaketooth Road, Road 3400, and Road 3406 formed the third cluster which identifies populations of *I. thompsonii*. Iron Mountain II and Road 333 represent mixed populations with members classified as *I. innominata* or *I. thompsonii*. *Iris innominata* has a more compact cluster (mean distance to cluster center 0.33), indicating that this species is more homogeneous than *I. douglasiana* (mean distance 0.56) and *I. thompsonii* (mean distance 0.45). Mean character values (\pm SE) for the three species are given in Table 2.

The discriminant analysis verified the classification of the thirteen

TABLE 2. MEAN VALUES (\pm SE) OF NUMERICAL CHARACTERS AND RATIOS FOR THREE *IRIS* SPECIES FROM SOUTHWESTERN OREGON AND NORTHERN CALIFORNIA. ¹Measurements are in mm. ²Not used in numerical programs.

	<i>I. douglasiana</i>	<i>I. innominata</i>	<i>I. thompsonii</i>
Characters ¹			
Yellow flowers	0.1 \pm 0.06	4.9 \pm 0.03	0.0 \pm 0.03
Purple flowers	4.7 \pm 0.09	0.0 \pm 0.00	4.7 \pm 0.10
Number of leaves	1.9 \pm 0.07	2.1 \pm 0.08	2.1 \pm 0.11
Leaf width	1.3 \pm 0.02	0.5 \pm 0.01	0.4 \pm 0.00
Number of flowers	3.3 \pm 0.89	1.0 \pm 0.00	1.1 \pm 0.05
Stem length ²	19.0 \pm 1.11	12.6 \pm 0.58	16.5 \pm 0.81
Bract length	7.7 \pm 0.15	4.2 \pm 0.08	4.5 \pm 0.09
Bract width	1.7 \pm 0.03	1.1 \pm 0.02	1.2 \pm 0.04
Petal length	5.7 \pm 0.08	4.3 \pm 0.05	4.7 \pm 0.08
Petal width	1.4 \pm 0.03	1.0 \pm 0.01	1.0 \pm 0.02
Sepal length	6.3 \pm 0.09	4.9 \pm 0.06	5.2 \pm 0.10
Sepal width	2.4 \pm 0.05	1.9 \pm 0.03	2.0 \pm 0.05
Stigma length	4.3 \pm 0.06	3.1 \pm 0.03	3.4 \pm 0.05
Stigma width	1.3 \pm 0.02	1.1 \pm 0.02	1.1 \pm 0.04
Stigma lobe length	1.3 \pm 0.02	1.1 \pm 0.00	1.2 \pm 0.01
Peduncle length	2.8 \pm 0.12	0.8 \pm 0.05	0.8 \pm 0.05
Perianth tube length	1.6 \pm 0.02	2.1 \pm 0.03	2.4 \pm 0.05
Ratios ²			
Bract length/width	4.7 \pm 0.13	3.7 \pm 0.09	3.8 \pm 0.13
Petal length/width	4.3 \pm 0.10	4.4 \pm 0.06	4.8 \pm 0.11
Sepal length/width	2.7 \pm 0.03	2.6 \pm 0.03	2.7 \pm 0.05
Stigma length/width	3.6 \pm 0.07	2.9 \pm 0.06	3.2 \pm 0.09

populations into three groups (Fig. 2). Again, Iron Mt. II and Road 333 were found to be mixed populations with both *I. innominata* and *I. thompsonii* present. The classification of the thirteen populations into three groups was found to be highly significant (F-statistic 336.9). The functions computed were found to be closely correlated to the groups discriminated as shown by the large values of the canonical correlations (0.988 and 0.976). Discriminant values show patterns similar to results from the cluster analysis, with *I. innominata* having the smallest range for discriminant values. Two populations, Snaketooth Road and Champion Park, had OTU's that were some distance from the group center (Fig. 2, a and b, respectively). These OTU's are considered to be variants within these populations. These three OTU's are not candidates for current hybridization, as the two populations from which they were collected are not presently sympatric with populations of other species and past hybridizations are not suspected as the other OTU's analyzed from the populations do not show evidence of intermediate character states (27 and 17 OTU's were analyzed from the Snaketooth and Champion Park populations, respectively).

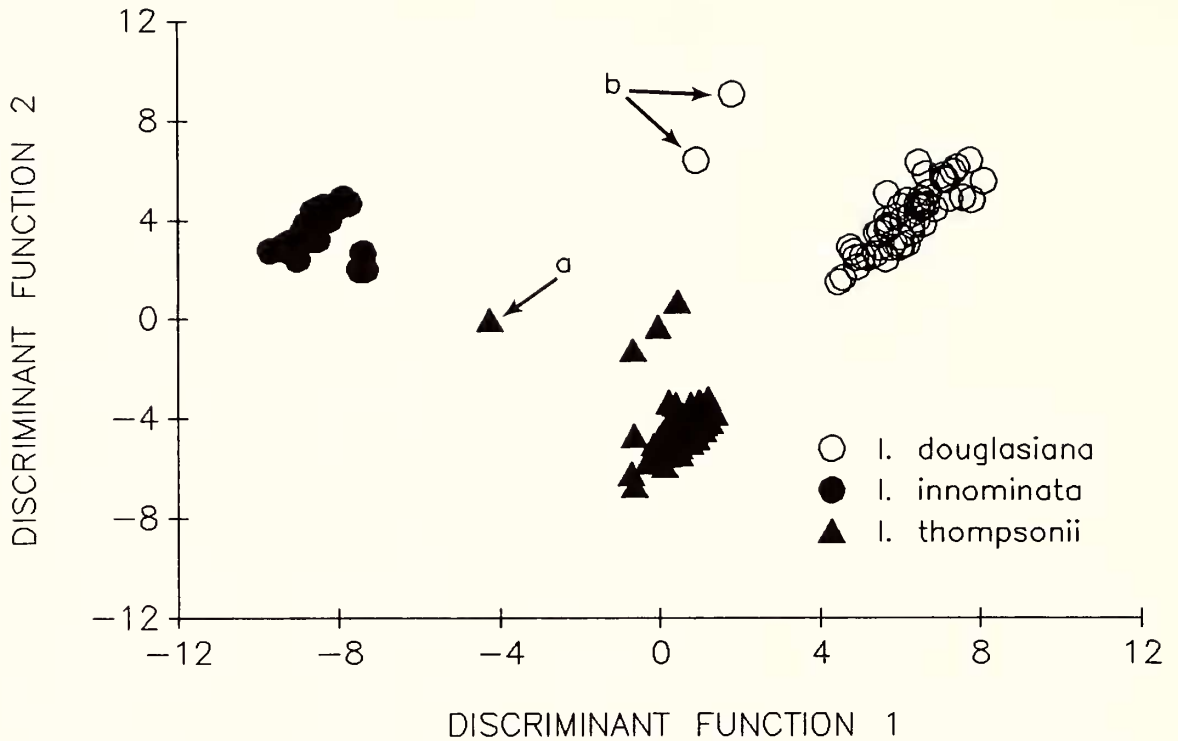


FIG. 2. Separation of three species of *Iris* from southwestern Oregon and northern California using SYSTAT DISCRIM. a. OTU from Snaketooth Road. b. OTU's from Champion Park.

Figure 3 illustrates the relationships of the populations studied. Based on discriminant and clustering data, the Iron Mt. and Rd. 333 populations have been subdivided into Iron Mt. II-i, Iron Mt. II-t, Road 333-i, and Road 333-t indicating the species present.

Flavonoid Studies. Fourteen flavonoid spots that are characteristic for the three species were resolved from the populations studied (Table 3). Four flavonoids are common to all three species. Pigment spots D5–D7 were found only in populations of *I. douglasiana*; I3, I4, and I7 in populations of *I. innominata*; and T1 and T2 in *I. thompsonii*. Two flavonoid spots (I1 and Y2) were found in populations of *I. innominata* and *I. thompsonii* but not in populations of *I. douglasiana*. Several additional flavonoid spots were also found in one or sometimes two populations of a taxon but are not considered here as they contribute no additional information. As indicated in Table 3, Champion Park did not contain two of the flavonoid spots that were present in other *I. douglasiana* populations studied.

DISCUSSION

Foster (1937) recognized three species in his survey and cited differences in flower color, perianth tube length, shape of perianth and spathes (bracts), and nature of cauline leaves as support for the recognition of *I. thompsonii* as a species separate from *I. innominata*.

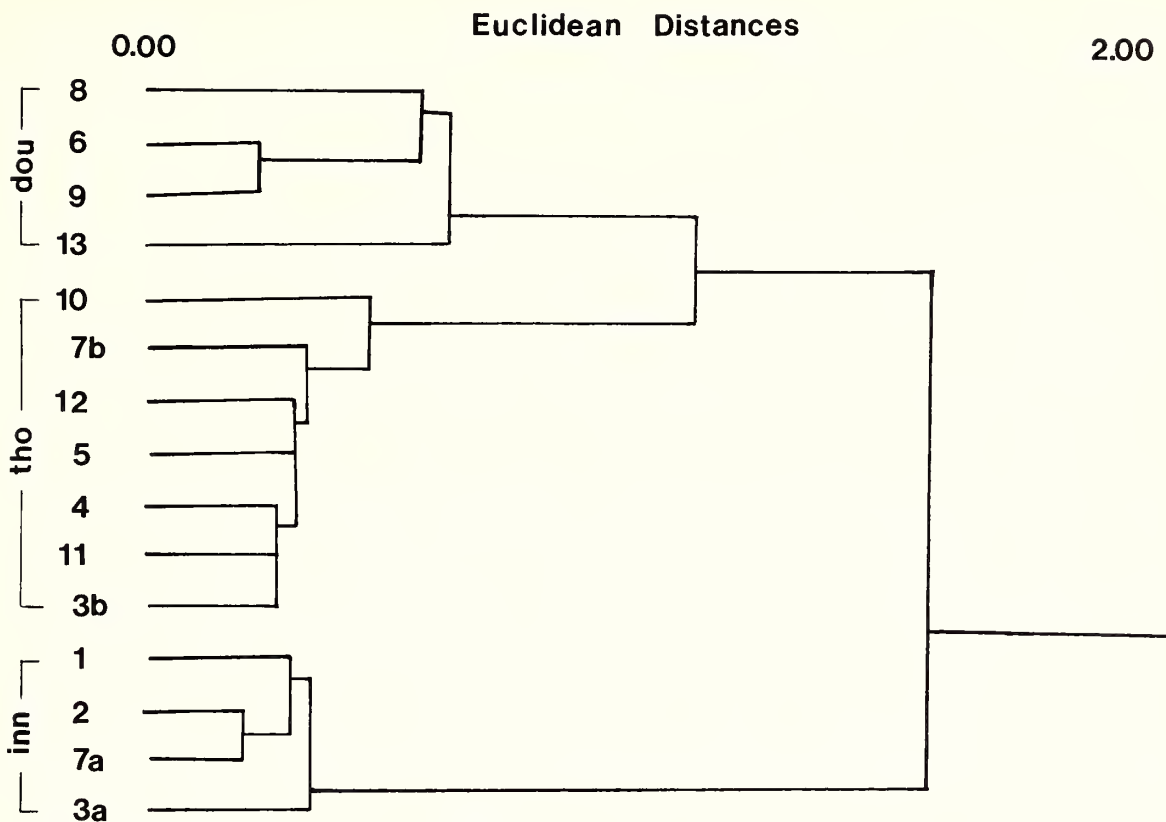


FIG. 3. Tree diagram of populations of three *Iris* species from southwestern Oregon and northern California using morphological characters and the SYSTAT JOIN algorithm. 1. Daphne Grove. 2. Iron Mountain I. 3a. Road 333-i. 3b. Road 333-t. 4. Road 3400. 5. Road 3406. 6. Cape Blanco. 7a. Iron Mountain II-i. 7b. Iron Mountain II-t. 8. Champion Park. 9. Meyers Creek. 10. Carpenterville. 11. Snaketooth Road. 12. Chetco River. 13. Smith River.

He indicated that the perianth tube of *I. thompsonii* was shorter than that of *I. innominata*. During this study it was determined that the perianth tube of *I. thompsonii* was longer than that of *I. innominata* and *I. douglasiana*. Foster's description was based on one herbarium specimen, which may account for the discrepancy between this study and his findings. During this study the petals, sepals, and stigmas of *I. thompsonii* were found to be longer relative to their width when compared to *I. innominata* (Table 2), supporting Foster's assertion that differences in perianth shape occur. Lenz (1958), in his revision of the Pacific Coast iris, considered *I. douglasiana* and *I. innominata* to be species, but proposed that *I. thompsonii* be retained within the yellow-flowered *I. innominata*. He considered the cream to purple *I. thompsonii* to be a color form or in some populations a hybrid between this species and the purple-flowered *I. douglasiana*. Clarkson (1962) concluded that *I. thompsonii* was of hybrid origin and occupied a habitat intermediate to *I. douglasiana* and *I. innominata*. He found that *I. innominata* was restricted to serpentine sites whereas *I. douglasiana* was found on non-serpentine sites. He postulated that *I. thompsonii* was able to

TABLE 3. TAXONOMIC DISTRIBUTION OF FLAVONOID SPOTS IN FLORAL PARTS OF THREE *IRIS* SPECIES FROM SOUTHWESTERN OREGON AND NORTHERN CALIFORNIA. ¹Champion Park population lacked pigment spots D5 and D6.

Species	Flavonoid spots													
	D1	D2	D3	D4	D5	D6	D7	I1	I3	I4	I7	Y2	T1	T2
<i>I. innominata</i>	X	X	X	X	—	—	—	X	X	X	X	X	—	—
<i>I. douglasiana</i> ¹	X	X	X	X	X	X	X	—	—	—	—	—	—	—
<i>I. thompsonii</i>	X	X	X	X	—	—	—	X	—	—	—	X	X	X

colonize sites intermediate to the habitats of the parental species. His study suggested that *I. thompsonii* should be recognized as a separate taxon although he did not favor species status for any of the three taxa. Clarkson had earlier proposed reducing all of the six Oregon members of the series to subspecific rank under *I. tenax*, the most widespread of the Oregon species (Clarkson 1959). He based this reduction in status on lack of "cytological barriers" and the presence of natural hybrids. His taxonomic treatment has not been generally accepted.

During field work it was found that *I. douglasiana* is restricted to a narrow band within 2 kilometers of the ocean (Fig. 1), usually on grassy headlands and in pastures. It is associated with well developed soils at most sites (the Meyers Creek population is adjacent to a large serpentine outcrop). *Iris innominata* was found to have a limited distribution in the northern portion of the study area. It occurred at higher elevations on rocky, sparsely vegetated sites. A greater portion of the study area was occupied by *I. thompsonii*. It was found in light shade on both grassy and gravelly sites. The three species are commonly found along roadsides, possibly because of the openness of such habitats. Although soil type was not ascertained during this study, observation of the soils and associated communities generally supports Clarkson's opinion that *I. innominata* is found on serpentine sites, *I. douglasiana* is found on non-serpentine sites, and *I. thompsonii* occupies intermediate sites.

Numerical data indicate that *I. innominata* is the most homogeneous species, *I. douglasiana* is the most variable of the species, and *I. thompsonii* has an intermediate level of variability. The level of variation is expressed both overall (Fig. 2 and average distance-to-cluster center) and in individual characters (Table 2) for the three species. Variation in flower color has been problematic in the taxonomy of these species (Lenz 1958, 1959a; Clarkson 1959). In the present study, it was found that *I. innominata* has butter yellow flowers and shows little variation in flower color, whereas both *I. thompsonii* and *I. douglasiana* (mainly purple-flowered species) show

variation in flower color. Plants with white, cream, grey, red, blue, and lavender flowers occur in some populations of *I. thompsonii* whereas plants with cream, blue, and lavender flowers occur in some *I. douglasiana* populations.

Hybridization among members of the series *Californicae* has been cited by several workers. Foster (1937) in his survey of the North American species of *Iris* cited the importance of crossing on speciation within the group. He suggested that the series is composed of several species-complexes. He considered *I. innominata* and *I. thompsonii* to be clearly allied and possibly best placed in a complex with *I. douglasiana*, *I. bracteata*, and *I. purdyi*. Due to geographical and morphological considerations, he did not feel that such a complex could be clearly delineated. Smith and Clarkson (1956) examined cytology and embryo development in artificial crosses between species within the series. They found that fertile hybrids were produced between all crosses except *I. tenuis*. *Iris tenuis* has been transferred to the subsection *Evansia* (Lenz 1959b) largely due to chromosome studies (*I. tenuis* has $2n=28$ chromosome numbers whereas all of the *Californicae* are uniformly $2n=40$). Morphological characters (Lenz 1959a; Clarkson 1959, 1962; Clarkson and Thompson 1961) and chemical and morphological characters (Carter and Brehm 1969) have been analyzed in naturally occurring hybrids within the series. These studies established that fertile hybrids were found in nature and that hybrids were intermediate except in flower color. The studies by Lenz, Clarkson, and Clarkson and Thompson included *I. innominata*, *I. douglasiana*, and *I. thompsonii*. Each of these studies concluded, based upon the intermediate morphology and variable flower color, that *I. thompsonii* was a probable hybrid of *I. douglasiana* and *I. innominata*.

The present study does not provide clear support for a hybrid origin for *I. thompsonii*. In most characters it is intermediate to the putative parents. However, it is smaller in leaf width and has a longer perianth tube than either parent (Table 2). Perianth tube length was found to be 150% as long as in *I. douglasiana* and 114% as long as in *I. innominata*. Perianth tube length is considered important in the taxonomy of the series. The series is often subdivided into species with long (greater than three cm), short (less than one cm), and intermediate (1.5–2.5 cm) perianth tubes. The three species investigated in this study consist of the entire intermediate group.

Results from numerical methods placed *I. thompsonii* closest to *I. douglasiana* (Figs. 2 and 3). Flavonoid data indicate that it may be close to *I. innominata*, as it shares two flavonoid pigments with that species that are not found in *I. douglasiana* (Table 3). The analysis of flavonoids for a diploid hybrid is predicted to result in a pigment profile intermediate to the two parents where pigments

common to both parents would be present but not all pigments would be represented. Such profiles have been well documented in natural hybrids of the genus *Baptisia* and summarized by Alston (1967). In the series *Californicae*, intermediate flavonoid profiles have been documented for natural hybrids of *I. tenax* and *I. chrysophylla* (Carter and Brehm 1969). If *I. thompsonii* is of hybrid origin, sufficient time may have elapsed for the development of a unique flavonoid pattern.

Although the potential for hybridization has been demonstrated by earlier studies (Smith and Clarkson 1956), no evidence of recent hybridization was found. In populations where the two species were found growing together (Iron Mt. II and Road 333), intermediate plants were not found. Hybridization events may be rare or gene flow may not be facilitated between hybrids and other individuals. Differences were found in phenology, with *I. thompsonii* populations blooming generally in April and May, *I. innominata* blooming in late May and June, and *I. douglasiana* blooming in June and July. Differences in habitat preferences and perianth tube length have been discussed above. These factors may also serve to reduce gene flow among the species.

In summary, this study found that three species are present within the study area: *I. douglasiana*, *I. innominata*, and *I. thompsonii*. Of these three species, the yellow-flowered *I. innominata* is the most homogeneous species and is limited in distribution. Purple-flowered *I. douglasiana* and *I. thompsonii* are more variable both in flower color and other characters. Although neither of these would be considered a widespread species, both have larger distributions than *I. innominata*. The larger overall size and greater number of flowers per inflorescence easily distinguishes *I. douglasiana* from *I. innominata* and *I. thompsonii*. The purple flowers and longer perianth tube, bracts, and perianth parts distinguish *I. thompsonii* from *I. innominata* (Table 2). Differences in interspecific variation were not demonstrated. Numerical data indicate that *I. douglasiana* and *I. thompsonii* are more closely allied than *I. innominata* is to either of the two species. However, flavonoid data argue for a closer relationship between *I. innominata* and *I. thompsonii*. Although clearly *I. thompsonii* should not be considered a color variant of *I. innominata* or an occasionally occurring hybrid between *I. douglasiana* and *I. innominata*, the origin of the species is more difficult to determine. The morphological and flavonoid data do not support the currently accepted hypothesis of a recent hybrid origin for the species, although speciation following a hybrid event is a possibility. The origin of *I. thompsonii* may be resolved with further studies involving different techniques and study of other members within the series.

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